The Recognition Concept of Species

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Abstract. Wallace's view of species has prevailed to this day in a modified form as the so-called Biological Species Concept or Isolation Concept of Species. This concept suffers from serious problems, since it cannot be made to accommodate the only Class I (empirically supported) Model of Speciation, Geographic or Allopatric Speciation. Problems arise and are outlined with the Class II Model of Speciation proposed to accommodate the Isolation Concept: Speciation by the reinforcement of Isolating Mechanisms. All these difficulties fall away if a relational concept of species is abandoned. The Recognition Concept of Species is outlined in some detail for the first time and the mode of allopatric speciation it determines is discussed. Its wide significance for various fields of population biology is outlined.

The traditional conception of nature was overthrown by Darwin in 1859, but the fundamental message has never really been understood. The old way of thinking and the new can never be reconciled, but efforts to do so continue to the present day and the results produce a warped and largely erroneous view of the living world. Ghiselin (1974): The economy of nature and the evolution of sex.

Introduction

When we trade in ideas in population biology, species constitute our currency. Their peculiar significance and universality was long ago appreciated by Darwin's mentor, Sir Charles Lyell: 'The ordinary naturalist is not sufficiently aware that, when dogmatizing on what species are, he is grappling with the whole question of the organic world and its connection with a time past and with man; that it involves the question of man and his relation to the brutes, of instinct, intelligence and reason, of Creation, transmutation and progressive improvement or development. Each set of geological questions and of ethological and zool.[1] and botan.[1] are parts of the great problem which is always assuming a new aspect.' (Wilson, 1970: 164).

Any view of species must be cast in genetical terms if it is to be useful in understanding the process of evolution, and it must be comprehensive enough to cover most eukaryotes including man. However, aiming to provide a concept that effectively encompasses the sweep of living forms from unicellular algae, through the fungi, plants and animals to man is indeed an ambitious enterprise. It is, therefore, not really surprising that an entirely satisfactory outcome has not yet been achieved. Like Mayr (1963: 426) I believe it is possible that it can be achieved, provided one is able to identify correctly the genetical species' fundamental basis.

In this paper I first consider the broad specifications necessary for any genetical concept of species, then examine the current paradigm and note its shortcomings and inconsistencies. Finally, I offer an alternative view in more detail than previously. This alternative is free from the difficulties that attend the prevailing Biological Species Concept and generates distinct testable predictions, with pervasive implications for all branches of population biology.

With space strictly limited, I here do no more than deal with the main ideas of the two alternative views of genetical species. This is not the place for the detailed documentation of the new Recognition Concept; this will require book-length treatment, as did the Isolation Concept in its day (Dobzhansky, 1937; Mayr, 1942). I have been obliged to restrict my consideration of the Isolation Concept (Biological Species Concept) to the views of the two Grand Masters, Dobzhansky and Mayr, and have neglected to use the views of other leaders such as Carson and his associates, White, Stebbins, Ayala, and others, despite their significance. Similarly I have been unable to do more than touch on species and speciation in Kingdoms other than Animalia. In particular, special attention will have to be devoted to what happens in plants in a future work. Their relative neglect here should not be taken as implying that I believe them to warrant no closer attention.

The Heart of the Genetical Species

The very heart of any genetical species concept, however it is conceived, is vividly revealed by Carson's (1957) apt phrase: 'The species as a field for gene recombination.' Dobzhansky seems to have had essentially the same idea in his mind when he spoke (1951) of the species as 'the most inclusive Mendelian population.' Both authors restricted the term to biparental sexual eukaryotes, but otherwise their view seems entirely non-controversial. Controversy, however, does arise over the way the following two questions should be answered.

1. What sets the limits to the field for gene recombination?
2. How do these limits arise *ab initio*?

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Various genetical species concepts are distinguished by the way they answer these two questions. The concepts to be outlined and examined here are the currently orthodox Biological Species Concept (= Isolation Concept), and the newer Recognition Concept of Species (Paterson, 1973, 1978). My aim is to demonstrate the inconsistencies involved in the former, and the advantages of the latter concept.

The Isolation Concept of Species

It was not until Dobzhansky coined the term 'isolating mechanisms' and devoted an entire chapter to them in his classic Genetics and the Origin of Species *(1937) that the full significance of these adaptations was recognized by evolutionists.* (Mayr, 1976: 129).

I refer to the prevailing concept of species as the Isolation Concept because this name explicitly specifies the way the field for gene recombination is supposed to be achieved, namely through the development of the *ad hoc* characters that were referred to by Dobzhansky (1935, 1937), and almost all later authors, as Isolating Mechanisms.

Thus, for Dobzhansky (1970: 357) 'Species are . . . systems of populations; the gene exchange between these systems is limited or prevented by a reproductive isolating mechanism or perhaps by a combination of several such mechanisms.' It will be noticed that in accordance with this view, a species is defined in terms of its relationship to other species, i.e., it is a *relational* concept, as has long been emphasized by Mayr (1942, 1963, 1970).

Mayr and Provine (1980: 34) expressed a similar view: 'The major intrinsic attribute characterizing a species is its set of isolating mechanisms that keeps it distinct from other species.' These quotations make it evident that both Dobzhansky and Mayr would have answered the first question raised above with: 'isolating mechanisms' (Mayr, 1976: 520).

If the isolating mechanisms do indeed set the limits of a field for gene recombination, the question arises as to how these characters are acquired by all members of the species. Two obvious circumstances could lead to the fixation of the alleles involved: chance in small isolated populations, and natural selection.

Alleles or chromosomal rearrangements can become fixed by chance even if they are somewhat disadvantageous as heterozygotes. This is clear because pairs of closely related species are known which differ from each other by the fixation of alternative chromosomal arrangements, such as paracentric or pericentric inversions, or by some form of translocation, all of which are more or less disadvantageous in the heterozygous state in most species.

The well-established, and now reasonably understood, phenomenon of pleiotropy is also important in understanding the spread of alleles under selection. In general an allele has more than one phenotypic effect. Some of these may be advantageous, some disadvantageous, and some almost neutral. For an allele to spread by selection, there must be a net selective advantage to it in the heterozygous state. To understand the fixation of an allele under selection, it is essential to understand the nature of its advantage. One would fail to understand how an allele became fixed if, for example, one was aware of only a disadvantageous phenotypic side-effect. This type of misjudgement is all too easy to make, since the most conspicuous phenotypic effect may not be the advantageous one, which might well be physiological in character, and therefore cryptic. Williams (1966) looked at pleiotropy from an evolutionary viewpoint, and restricted the word *function* to apply to the principal advantageous phenotypic effect of an allele. All the remaining consequences, whether advantageous, disadvantageous, or somewhat less advantageous, he named *effects*. Thus, in seeking to elucidate the evolution of a species-specific character, we need first to decide whether it was fixed stochastically or by natural selection. If the latter, we need to identify the function it serves. This may be far from obvious, and our judgement may well be coloured by our point of view. For example, if we find two sympatric, congeneric species which breed at quite distinct times of the year, an evolutionist might seek a function in terms of *reproductive isolation*, and call the character an isolating mechanism. On the other hand, an ecologist might point out that each species breeds when its food is most abundant and might not even notice that it has any influence on the possibility of the members of the two populations hybridizing. Is reproductive isolation the character's *function* or merely an *effect*? I find it doubtful, to put it very mildly, that any 'premating isolating mechanism' was ever evolved to serve the function of reproductively isolating the members of one species from those of another. To me, the isolating role seems always to be better accounted for if it is viewed as an effect. Quite certainly the 'postmating isolating mechanisms' isolate only incidentally, as was made abundantly clear by Darwin (1859: 245 ff.), though a remarkable number of modern population geneticists have failed to see his point. With this argument in mind we can attend to the second question.

Accepting that the field of gene recombination is delimited by the isolating mechanisms imposes restrictions on the answering of the second question: 'How do these limits [isolating mechanisms] arise *ab initio*?' These constraints demand that characters evolved to function as isolating mechanisms must arise in sympatry or parapatry. But this conflicts with the empirical observation that the only Class I (i.e., empirically supported) mode of speciation is speciation in allopatry (Paterson, 1981). The difficulties arising from this conflict will be illustrated with quotations from the literature.

The two seminal advocates of the Isolation Concept, Dobzhansky and Mayr, have both been surprisingly inconsistent in their writings on isolating mechanisms, which makes it difficult to be certain what their concepts actually are. In part this was due to the conflation of the different species concepts (Taxonomic, Isolation and Recognition) (e.g., Mayr, 1963: 89, 95), but other conceptual problems are also involved. Even in his very first theoretical paper on species, Dobzhansky had difficulties. In discussing isolating mechanisms he wrote (1935: 349): 'Although the mechanisms preventing free and unlimited interbreeding of related forms are as yet little understood, it is already clear enough that a large number of very different mechanisms of this kind are functioning in nature. This diversity of the isolating mechanisms is in itself remarkable and difficult to explain. It is unclear how such mechanisms can be created at all by natural selection, that is what use the organism derives directly from their development. We are almost forced to conjecture that the isolating mechanisms are merely by-products of some other differences between the organisms in question, these latter differences having some adaptive value and consequently being subject to natural selection.' It will be noticed how the acceptance of speciation in allopatry compels authors to invoke pleiotropy as a basis for changing the limits of the field for gene recombination. But of course, isolating mechanisms can then no longer be called *mechanisms*, or be regarded as *ad hoc*, nor can speciation be regarded as adaptive *per se*. This is the price authors have been reluctant to pay.

The following passage shows that in 1970 Dobzhansky still had fundamental difficulties with this problem (p. 376): 'The question naturally presents itself, what causes bring about the development of reproductive isolating mechanisms? Two hypothetical answers have been proposed. First, reproductive isolation is a by-product of the accumulation of genetic differences between the diverging races . . . Second, the isolation is built up by natural selection, when and if the gene exchange between the diverging populations generates recombination products of low fitness . . . These two hypotheses are not mutually exclusive. Needless disputes have arisen because they were mistakenly treated as alternative.'

In practice the problem cannot so readily be disposed of. The assertion that these two hypotheses are not alternatives seems to me to be impossible to sustain; the first does not invoke any direct selection for 'reproductive isolation', while the second does. This is a very fundamental difference between them, as each has very different consequences for evolutionary theory.

In 1950 Dobzhansky wrote (see also Dobzhansky, 1976: 104): 'The integration of individuals into Mendelian populations, into sexual supraorganisms if you will, is an evolutionary adaptation. The further integration of elementary Mendelian populations into populations of higher orders, such as races and species, is likewise adaptive. It can be shown that formation of races and species has become necessary owing to the great diversity of environments found on our planet.' This statement provides us with an insight on how Dobzhansky conceived the role of species; why he required species to be the direct products of natural selection (cf. Mayr, 1949: 284, for a comparable statement). In the following passage (Dobzhansky, 1940), his bias in favour of the selection hypothesis clearly shows through: 'Another difficulty is with species isolated on oceanic islands or in similar situations. If the geographical barriers between races are secure enough, the precondition for the development of physiological [= reproductive] isolation is absent. Precisely how serious is this difficulty is not clear'. In the third edition of his book (Dobzhansky, 1951: 208) we find: 'Isolating mechanisms encountered in nature appear to be *ad hoc* contrivances which prevent the exchange of genes between nascent species, rather than incongruities originating in accidental changes in the gene functions.' A clear reluctance to rely on pleiotropy in isolation is evident.

Inevitably, Mayr (1963: 548; see also p. 109) was plagued by the same problem: 'They are *ad hoc* mechanisms. It is therefore somewhat difficult to comprehend how isolating mechanisms can evolve in isolated populations.' Mayr's problem was particularly acute since he is an ardent advocate of geographical or allopatric speciation. I have recently (1981: 113) emphasized that there is much observational evidence for the origin of new species in total isolation (Mayr, 1942, 1963), and that there is no such support for any other model of speciation. Dobzhansky's favoured model of speciation through the reinforcement of isolating mechanisms under natural selection is one among many for which there is no convincing evidence. Even after some 40 years of active research, the support for speciation by reinforcement today is still both meagre and equivocal (Loftus-Hills, 1975; Paterson, 1978, 1981, 1982*a*).

These few difficulties alone seem sufficient to falsify the isolation concept of species, and yet they constitute but some of its problems.

The Isolation Concept was supported by Wallace (1889) but not by Darwin. Later it was further elaborated by Gulick (1905), in remarkably modern terms, who appears to have anticipated Dobzhansky to a considerable extent. Both Robson (1928) and Fisher (1930) supported the Isolation Concept. Doubtless, however, the concept's wide support stems from Dobzhansky's effective advocacy (1937, 1940, 1970).

As already stated, Dobzhansky was aware of problems and inconsistencies with the concept in 1935, and yet he adhered to it consistently throughout his life. It is important to ask why he should have done so. In a wider context, the very general, unquestioning support the Isolation Concept has received is suspicious. To me it suggests that this favour might stem from deep-seated biases inherent in our Western cultural background (cf. Masters *et al.*, 1984; Paterson, 1982*b*). One obvious source of bias is the creation stories in the Book of Genesis. That this has been, and indeed is, an important source of prejudice was made clear by Darwin at the beginning of his chapter on Hybridism (Darwin, 1859: 245): 'The view generally entertained by naturalists is that species . . . have been specially endowed with the quality of sterility in order to prevent the confusion of all organic forms.'

Support for this contention can be gleaned from Ellegard (1958), who records the opinions of nineteenth century general readers and scientists alike: 'God forbids hybrids to breed', 'the sterility of true hybrids affords another evidence of the jealousy with which the Creator regards all attempts to introduce confusion into His perfect plan', etc. From this widely held viewpoint, a species is seen as a group of organisms descended from the same original created pair.

Another, even older, source of bias in favour of the Isolation Concept stems from prehistoric attitudes to 'purity of stock' and 'purity of line', engendered by the practices of ancient plant and animal breeders. The introduction of managed breeding programmes undoubtedly revolutionized man's whole way of life, and, one would think, influenced his language by enriching its vocabulary and imagery. In English, notice how approbative are words such as 'pure', 'purebred', 'thoroughbred', and how pejorative are those like 'mongrel', 'bastard', 'halfbreed' and 'hybrid'. Such cultural biases, which act subtly, almost subliminally, through the vocabulary and imagery of languages, might well predispose the unwary to favour ideas like that of 'isolating mechanisms' with the role of 'protecting the integrity of species'. When Dobzhansky introduced the Isolation Concept in 1937 it was accepted almost without resistance. This acceptance is in sharp contrast to the usual opposition that greets new ideas (cf. Kuhn, 1970), and could well have been due to these cultural predisposing factors.

Thus, problems of function, logic and consistency beset the Isolation Concept.

The Recognition Concept of Species

It is no use for a species to have individuals of two sexes, supplied with reproductive apparatus mutually adapted for their propogation, if the individuals are not endowed with suitable genetically determined impulses. The potential parents must also have instincts, prompting them to desire one another and to provide for the resulting young such care as they need for their survival. (Darlington, 1964: 335).

It is rather obvious that the complex act of fertilization, which is an essential part of sex, will not occur fortuitously, as is recognized by Darlington in the quotation above. The physiologist J. Z. Young (1975) provided an independent view of the same situation: 'To ensure that reproduction occurs at times of the year when young are likely to survive, the slowly operating chemical signalling of the endocrine system is used . . . Control through the nervous system is important, however, for the performance of reproductive actions in relation to other members of the species, and in all mammals there are communication signs by which individuals recognize others of the same or opposite sex and elicit appropriate mating reactions from them . . . Further, there are *secondary sexual characters* providing signals ensuring that the sexes meet and pair'.

Among evolutionists, recognition of the existence of a fertilization system in all biparental eukaryotes is general, though its full significance is seldom emphasized. Thus, both Dobzhansky (1951: 184) and Mayr (1963: 95) were aware of its existence. What has not been recognized and emphasized is that the form of the fertilization system accounts for the delineation of 'fields for gene recombination' in a simple, rational, and yet comprehensively adequate way. Mayr (1963: 20) in fact rejects this approach explicitly in favour of a relational concept: 'Species are more unequivocally defined by their relation to non-conspecific populations ("isolation") than by the relation of conspecific individuals to each other. The decisive criterion is not the fertility of individuals but the reproductive isolation of populations.'

True sex is found only in biparental, eukaryotic organisms. Despite considerable variation in detail, sexual cycles always involve the two complex processes of meiosis and fertilization (Lewis and John, 1964). Successful fertilization in even the simplest of unicellular eukaryotes requires the assistance of a series of adaptations which constitute what might be called the Fertilization System of the organism (Fig. 1).

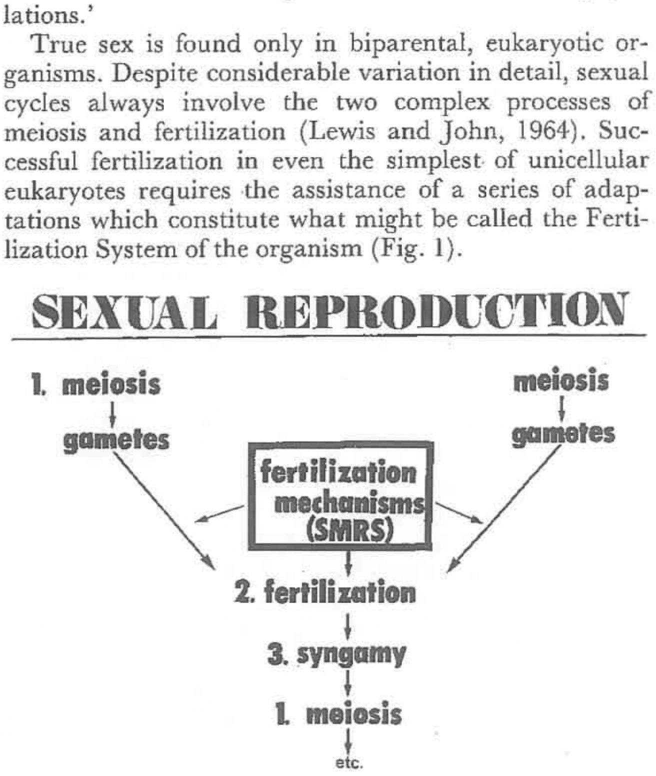

Fig. 1. Sexual cycle in a biparental eukaryote.

Each fertilization system comprises a number of components, each adapted to fulfill a subsidiary proximate function, which contributes to the ultimate function of bringing about fertilization while the organism occupies its normal habitat.

Fertilization systems are also adapted to the circumstances imposed by the organism's 'way-of-life' (i.e., whether sessile, motile, nocturnal, diurnal, etc.). Thus, motile organisms have a special requirement for a subset of characters of the fertilization system that serve the function of bringing motile mating partners together as a necessary preliminary to the ultimate achievement of fertilization and syngamy.

This subset of adaptations, which are involved in signalling between mating partners or their cells, constitutes the Specific-Mate Recognition System or SMRS (Fig. 2) (Paterson, 1978, 1980). I have chosen to use 'specific-mate' instead of simply 'mate', because it is important to distinguish between the process with which I am concerned and the quite different kind of mate recognition, 'individual mate recognition'. I also avoid the common term 'species recognition' because the process with which I am concerned most certainly does not involve 'species recognition', a strictly philosophical process, but the recognition of an appropriate mating partner. ('Appropriate' here implies no more than an individual of opposite sex drawn from the same 'field for gene recombination'.)

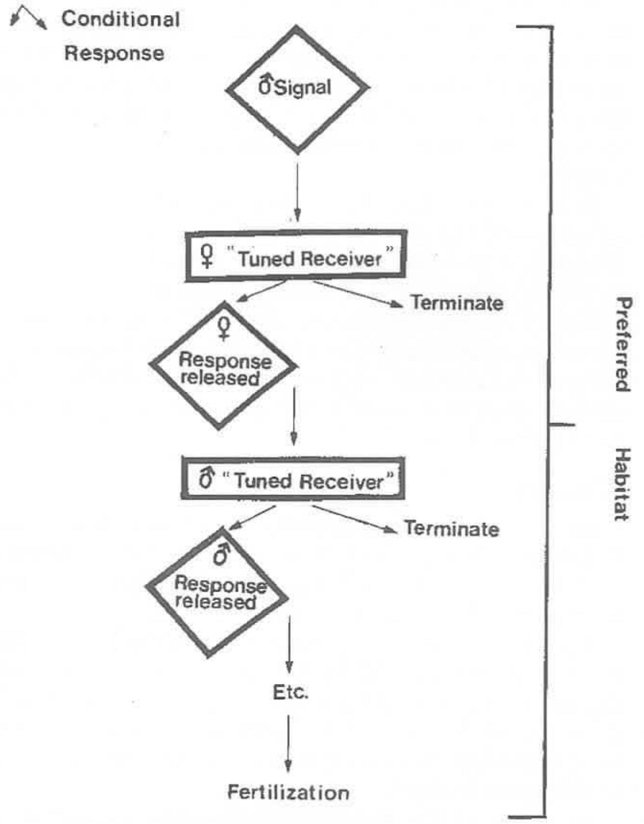

Fig. 2. Simplified diagram illustrating the form of the Specific-Mate Recognition System (SMRS) as a coadapted signal-response reaction chain. A more realistic representation was given by Morris (1970: 338).

The response of one mating partner to a signal from the other is here regarded as an act of *recognition* (Paterson, 1982*a*). Recognition is thus a specific response by one partner to a specific signal from the other. This process might be compared to the recognition of a specific antigen by its specific antibody, and hybridization involves a process having something in common with a cross-reaction. I strongly emphasize that I imply no act of judgement, and no act of choice on the part of the responding partner (Paterson, 1982*a*).

As a working hypothesis I have assumed that all steps in a fertilization system have evolved to serve a particular role. In other words, I assume that all components are adaptations, or, at least, were adaptations, in the strict sense of Williams (1966). It is possible to sustain such a view if one examines the well-analysed 'courtships' of the three-spined and ten-spined sticklebacks (Tinbergen, 1951; Morris, 1970), though, admittedly, the case is less diagrammatically clear in species which have not yet been as closely analysed (e.g., the ducks).

In sessile organisms the SMRS assumes a much less prominent role; positive assortative mating is determined in these organisms by other adaptations of the fertilization system. The sex cells of sessile biparental eukaryotes are transported by various agencies including wind, water, insects, birds and mammals (e.g., bats). In sessile organisms, as in motile, the fertilization system is closely adapted to the conditions of the organism's way-of-life and normal habitat. This becomes strikingly evident when one compares, for example, the fertilization systems of two very distantly related organisms from the intertidal zone of a rocky shore. The fertilization system of an oyster (or a mussel) and of a species of brown alga are much more similar than are the systems of the oyster and its motile predatory fellow mollusc, *Sepia officinalis* (Tinbergen, 1939). The fertilization system of the squid, in turn, resembles much more closely the systems of some fish (Packard, 1972; Ghiselin, 1974).

Among angiosperms the SMRS is limited to interactions such as between the pollen and the stigma (Clarke and Knox, 1978), and in sessile animals it may be restricted to the recognition of the sperm by the ovum. Among orchids, several species, even of different genera, may share a common SMRS. This is evident from the observation that fertile experimental crosses can be made between them. In these species the 'fields for gene recombination' are determined by the fertilization mechanisms other than those of the SMRS. In orchids they usually involve the attraction and exploitation of a particular insect species as a vector of pollen (e.g., the Western Australian slipper orchid, *Cryptostylus ovata*, Erickson, 1951). Darwin, in the introductory sentences of his book (1862) on the pollination of orchids by insects, expresses a view in perfect agreement with the Recognition Concept: 'The object of the following work is to show that the contrivances by which the orchids are fertilized are varied and almost as perfect as any of the most beautiful adaptations in the animal kingdom; and, secondly, to show that these contrivances have for their main object the fertilization of the flowers with pollen brought by insects from a distant plant.'

Taking such facts as these into account, it is clear that the limits to a 'field for gene recombination' can be set by the shared fertilization system of members of a population of organisms alone. It is the fertilization system which leads to the positive assortative mating that delimits the field.

We can, therefore, regard as a species that most inclusive population of individual biparental organisms which share a common fertilization system.

I now turn to the second question: How does a new fertilization system, and hence a new species, arise *ab initio*?

In terms of fitness, a mate is a crucial resource. Mate acquisition is, thus, as important an adaptive process as is avoidance of predators, the ability to find a refuge, or the acquisition of food. As with these other adaptive characters, the characters of the fertilization system are adapted to the circumstances impinging on the organism in its normal habitat. While members of a species are occupying their normal habitat the characters of the fertilization system, as well as their other adaptive characters, are all maintained under stabilizing selection. This means that while biparental eukaryotes remain in their normal habitats, their adaptive characters remain largely buffered from directional change.

From this insight, it is evident that for speciation to occur the buffering of adaptive characters must be over-come, so that a new constellation of adaptive character-states can evolve. This is most likely to happen if a small population (Paterson and Macnamara, 1984: 315) of conspecific individuals becomes displaced into, and restricted to, a new habitat. The isolation envisaged here is allopatric isolation induced by extrinsic circumstances, such as a flock of birds being blown out to sea onto an island on which their normal habitat is not to be found. Many other scenarios might be invoked according to particular circumstances. Any adaptive characters, including those of the fertilization system, which are now less well adapted, will become subject to directional selection. Eventually, when the character-states of the population members have shifted under selection, etc., to become appropriate and effective under the new conditions, they will return once more to the control of stabilizing selection. At this point we say that the individual organisms of the population are adapted to the new habitat. Speciation will also have occurred if the new fertilization system has become sufficiently different from that of the members of the parent population, for then the new fertilization system will delimit a new field for gene recombination. At present the time needed for such speciation to occur is essentially unknown, but it may be relatively short (Greenwood, 1965).

The adaptation of all the adaptive characters to the conditions of the new habitat also determines a new 'niche' for the daughter species, and the stabilizing selection within the normal habitat stabilizes these ecological characteristics as well. It is clear that speciation and the acquisition of a new niche are part of the same process of adaptation to a new habitat. There is no special process of cladogenesis; speciation is an incidental *effect* resulting from the adaptation of the characters of the fertilization system, among others, to a new habitat, or way-of-life.

Although this view of speciation must be classified with Mayr's model of geographical speciation (Mayr, 1963) it should be appreciated that they are not identical. Because Mayr conceives species in terms of reproductive isolation, he is obliged to invoke the pleiotropic modification of 'isolating mechanisms' in allopatry to account for geographic speciation. No such problem faces the advocates of the new species concept. Since the characters of the fertilization system are clearly adaptive in relation to the species' normal habitat, speciation results from their adaptation to the conditions in the new habitat (see below).

Despite a major role being assigned to natural selection in the model of speciation discussed above, I do not count myself in the ranks of Kimura's 'naive panselectionists'. I do accept an important role for stochastic processes. This view can scarcely be avoided if one notices that closely related species may differ in possessing fixed alternative chromosomal arrangements (see above).

The correlation of fixed chromosome rearrangements with speciation cannot be regarded as evidence for a causal connection between the two events as White (1978) has argued (cf. Carson *et al.*, 1967; Paterson, 1981).

A small population isolated in a new habitat will more often than not become extinct. However, should it survive over a number of generations it is likely to remain small because its members are ill-adapted and are under directional selection. The population is likely to increase only after its members have adapted to the new conditions.

It is unlikely that the characters of the SMRS can adapt quickly to new conditions. This is because the coadaptation that exists between the mating partners with respect to signals and receivers constitutes an effective buffer to change (Paterson, 1978). The signal and receiver can only change in small steps, with coadaptation being re-established after each step. The details of this process deserve a more comprehensive treatment than can be offered here.

Discussion

In reviewing the consequences of the Recognition Concept, the first thing to consider is the proposition that the Isolation and Recognition Concepts of species are merely 'the two sides of the same coin'.

According to the proponents of the Isolation Concept, species are determined by the functioning of the isolating mechanisms; that is, species are defined relationally in terms of Reproductive Isolation. Leading workers have regarded species explicitly, though inconsistently, as 'adaptive devices'.

In terms of the Recognition Concept, on the other hand, species are determined by the functioning of fertilization mechanisms; species are not defined relationally but independently, since, of necessity, all sexual organisms must possess an effective fertilization system. Species are seen as incidental consequences of adaptive evolution.

Applying the two concepts in turn to a newly arisen autotetraploid (see also Paterson, 1981) in a population of an outbreeding diploid angiosperm will serve to show that they are in fact quite distinct, and lead to quite different expectations. The situation described is generally accepted as a case of 'instantaneous speciation' by advocates of the Isolation Concept (e.g., by Mayr, 1963: 439, 448), because the tetraploid individuals are 'reproductively isolated' from the parental diploid population. In genetical terms, however, the gene pool of the tetraploids is merely a subset of the gene pool of the diploids. Accordingly, 'mating' is likely to occur at random. If this is considered in the light of population genetic theory, it will be seen that we are here dealing with an example of heterozygote disadvantage. The deterministic algebra makes it abundantly clear that, under the conditions outlined above, the tetraploid population would be rapidly eliminated. Inability to coexist is scarcely a criterion for a species in population genetics.

On the other hand, if the Recognition Concept is applied to this situation, the conclusion is inevitably reached that the two populations are conspecific because they share a common fertilization system. Natural selection, as shown above, thus eliminates the cause of the heterozygote disadvantage within the single species.

Besides revealing the distinctness of the two concepts, this scenario underlines a point which is not generally appreciated by evolutionists. This is that two populations that share a common SMRS cannot coexist if they are technically 'reproductively isolated' by 'sterility' alone (Paterson, 1968). In such a case, with complete interpopulation sterility ($s = 1$), the less common population will rapidly disappear (Paterson, 1978); but if the heterozygote disadvantage is less complete (i.e., if the coefficient of selection, s, is less than 1 but greater than 0), natural selection will act to eliminate the allele or chromosome rearrangement that is causing the hybrid disadvantage. Under these conditions, the 'interpopulation sterility' is thus an intraspecific phenomenon, comparable to the phenomenon of 'self-incompatibility' in plants (Clarke and Knox, 1978).

An example from animals is the well-known *Drosophila paulistorum* (Dobzhansky, 1970). Subpopulations are often semi-intersterile, despite sharing a common SMRS (in some cases they mate at random). The infertility is due to the interaction of the host genome with that of symbiotic mycoplasms in the gonads. In accordance with the Recognition Concept these subpopulations are conspecific, but Dobzhansky interpreted them as 'semi-species'. A comparable situation is found in the mosquito species *Culex molestus* Forskal of the *Culex pipiens* complex. The symbionts in this case are rickettsias (Irving-Bell, 1983; Miles, 1977). Some of these cases, at least, are laboratory artifacts arising from 'bottlenecks' in the colonies. Studies with fresh material from the field should be done in both complexes. Theoretical models of 'sympatric speciation' which depend on one or other form of 'sterility' (heterozygote disadvantage) are fairly widely accepted by evolutionists. But, again, in many cases they do not even constitute speciation according to the Recognition Concept because both populations in these models share a common fertilization system. Summarizing this point: under the Recognition Concept, all phenomena covered by the category 'postmating isolating mechanisms' (Mayr, 1963) are incidental to delineating species, since they have nothing to do with bringing about fertilization.

It has been shown that the Recognition Concept is not simply the 'obverse side of the same coin' as the Isolation Concept, and some of the logical and interpretive difficulties of the Isolation Concept have been enumerated. How well does the Recognition Concept accommodate currently debated ideas in population biology?

Reporting on the recent Chicago Macroevolution Conference, Maynard Smith (1981) made the following comment on the pattern of evolutionary change known as the punctuated equilibria model (Eldredge and Gould, 1972): 'As a geneticist I was left with the impression that the "sudden" appearance of a new species called for no new explanations, but that stasis may do.' In fact the Recognition Concept, and the mode of allopatric speciation it specifies, account for all aspects of the punctuated equilibria model very satisfactorily. The equilibrium is well explained by the stabilizing selection due to the coadaptation of the SMRS between the mating partners in their normal habitat, as has been explained. The 'sudden appearance' of new species fits a speciation model in which small isolated populations develop into new species, and grow in population numbers only after stabilizing selection is again in effect on the new species. The best illustration of these events that I know of from the fossil record is Coope's (1979) documentation of Cenozoic beetles moving with their habitat. The Isolation Concept does not lead one to expect equilibrium following a speciation event, as Maynard Smith's comment implies.

A point of special interest is that the Recognition Concept leads one to expect that in those species where some of the SMRS signals are preserved (e.g., horns or antlers), the fossil record is likely to illustrate punctuated equilibria with least ambiguity (Paterson, 1982*a*; Vrba, 1984).

The stability of adaptive characters expected under the Recognition Concept is relevant to the assessment of Van Valen's (1973) Red Queen Hypothesis (see Paterson, 1982*a*). The Recognition Concept and Coope's observations on fossil beetle populations suggest that Van Valen's expectation that natural selection acts mainly 'to enable the organisms to maintain their state of adaptation rather than to improve it' is not generally valid and may only apply under special circumstances. If Van Valen's Hypothesis was, in fact, realistically conceived, the punctuated equilibria pattern would not be expected as an outcome.

It is not always appreciated that the nature of species and the way speciation occurs have a fundamental role in any attempt at understanding the structure of communities and ecosystems. This is because most ecologists and population biologists attribute the fundamental causal role of patterns in nature to interspecific competition. However, in recent years a number of workers have come to question the critical role attributed to interspecific competition (e.g., Andrewartha and Birch, 1954; Wiens, 1977; Connell, 1980; Walter, Hulley and Craig, 1984). The field is too large to review in detail here, but it should be noticed that no emphasis was placed on interspecific competition as an environmental factor when considering how speciation occurs. Generally speaking, I agree that interspecific competition lacks the credentials of a 'motor' for evolutionary change. After much study there are still no really compelling examples of character displacement (Grine, 1981). While adaptation to a habitat and the coadaptation of the male and female parts of the SMRS are constraints, interspecific competition exerts only intermittent selective pressure on members of a species. Therefore, the evident stability of form in many species in space and time (see discussion above) with respect to adaptive characters does not favour interspecific competition as a selective force to account for 'niche' characteristics.

If speciation occurs as postulated above under the Recogniton Concept, then we obtain a radically different picture of how the structures of communities and ecosystems emerge. The normal habitat of a species is likely to approximate closely to that in which it arose. Similarly, the adaptive characters that were fixed in the original small isolate were subsequently stabilized in a number of ways, including stabilizing selection within the normal habitat of the species (cf. Coope, 1979). The increase in numbers of the original small population which speciated also constitutes a buffer to change. Accordingly, members of sympatric species do not come to 'partition resources' in an *ad hoc* manner. Character displacement is not expected according to this model, and it is not surprising that clear-cut cases are virtually non-existent. Species characteristics (fertilization system, niche characteristics, etc.) are expected to be largely stabilized throughout the range of the species. These expectations contrast strongly with those generated by interspecific competition theory, as Walter, Hulley and Craig (1984) have emphasized.

Although many important consequences could be added to the few examined in this discussion, only one other will be emphasized: the bearing the Recognition Concept has on how we look at man.

The Isolation Concept has a very definite teleological flavour to it (Paterson, 1982*b*). Species are seen as 'adaptive devices', and speciation is considered a process of adaptation by the leaders in the field. Isolating mechanisms are said to be *ad hoc* devices evolved to protect the integrity of a species. Such statements are teleological, or imply the involvement of group selection, or both.

In contrast, the Recognition Concept is free of teleological commitment and invokes only individual selection, as with Darwin's view (1859). Darwin conceived species in terms of structure, just as taxonomists did. He saw no essential difference between species and varieties. He believed that both arose in the same way, under natural selection. Inadequate though his view of species was, Darwin's view of speciation was detailed enough for us to see that he accepted that species arise as incidental consequences of adaptation. This was perhaps the most revolutionary conclusion in a revolutionary text, yet it is seldom stressed or even appreciated except by philosophers. Here it is emphasized by Hull (1973: 55): 'Galileo and Newton replaced one physical theory with another, but they left the teleological world-picture intact. The findings of the paleontologists and geologists had necessitated a reinterpretation of Genesis. But it was Darwin who finally forced scientists to realize just how trivial teleology had become in their hands. The change in scientific thought marked by the appearance of the *Origin of Species* was so fundamental that it certainly deserves the title conceptual revolution.' In the same vein, Thomas Kuhn (1970: 172) said: 'For many men the abolition of that teleological kind of evolution was the most significant and least palatable of Darwin's suggestions. The *Origin of Species* recognized no goal set either by God or nature.'

Thus, in sharp contrast to the Isolation Concept, the Recognition Concept is in complete accord with the revolutionary view of Darwin as far as it went. Moreover, the Recognition Concept emphasizes the incidental nature of speciation and expresses it in genetical terms, besides providing a genetical concept of species. Applied to man the concept is equally appropriate.

It was pointed out above that any comprehensive view of species must be able to deal satisfactorily with the question: What sets the limits to the field of gene recombination in man? In applying the Isolation Concept to man, a number of problems arise. Authors never seem to identify the isolating mechanisms that are supposed to delimit the field. Perhaps there are none, in accordance with this statement by Mayr (1963: 109): 'Where no other closely related species occur, all courtship signals [= "ethological isolating mechanisms"] can "afford" to be general, nonspecific, and variable.' However, I find Mayr's assertion to be poorly supported empirically (Paterson, 1978). I believe that Mayr wrote these words with a case such as the mallard and pintail ducks and some of their insular congeners in mind (Lack, 1974). It is hypothesized that the mallard and pintail are markedly sexually dimorphic in the Holarctic Region to isolate them reproductively from their many close congeners with which they are sympatric. On a number of islands such as Hawaii, Kerguellan, South Georgia and the Falkland Islands monomorphic relatives exist which are allopatric from all close congeneric species. It is presumed that they can here 'afford' to relax their 'isolating mechanisms'. In 1978 I pointed out that in Africa, Australia and North America, a number of monomorphic relatives of the mallard and pintail coexist without requiring the striking sexual dimorphism of their close relatives of the Holarctic, which weakens the case considerably (see also Weller, 1980: 68). It is further weakened when one notices that species with no close relatives on earth (e.g., the ostrich, the hamerkop (*Scopus umbretta*), the Madagascan partridge (*Margaroperdis madagascariensis*), etc.) nevertheless possess complex courtships. Thus, I believe the case for applying Mayr's statement to man is not convincing.

No such problem occurs in applying the Recognition Concept to *Homo sapiens*. This is not the place to analyse the SMRS of man in detail, and so I shall merely provide an independent and appealing lay statement of its existence by the psychologist Abraham Maslow (1970: 195): 'It is not the welfare of the species, or the task of reproduction, or the future development of mankind that attracts people to each other . . . it is basically an enjoyment and a delight, which is another thing altogether.'

The Isolation Concept in its complete form was presented for testing in 1940. Today it is still logically unsatisfactory, and in virtually all accounts it is intricately conflated with either or both the Recognition Concept and a morphological concept of species. Identifying the Recognition Concept as fundamentally different from the Isolation Concept enables us to design stringent tests in attempts at refuting the one or the other. This is definite scientific progress. My earnest hope is that it will reduce the prevailing fog and induce new life into that very significant biological discipline once called by Ernst Mayr the Science of Species.

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References

Andrewartha, H. G. and Birch, L. C., 1954. *The distribution and abundance of animals.* University of Chicago Press, Chicago.

Carson, L. H., 1957. The species as a field for gene recombination. *In:* Mayr, E., ed., *The species problem,* pp. 23–38. American Association for the Advancement of Science, Publication No. 50, Washington.

Carson, L. H., Clayton, F. E. and Stalker, H. D., 1967. Karyotypic stability and speciation in Hawaiian *Drosophila. Proceedings of the National Academy of Science of Washington* **57**: 1280–1285.

Clarke, A. E. and Knox, R. B., 1978. Cell recognition in flowering plants. *Quarterly Review of Biology* **53**: 3–28.

Connell, J. H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35**: 131–138.

Coope, G. R., 1979. Late Cenozoic fossil Coleoptera: evolution, biogeography, and ecology. *Annual Review of Ecology and Systematics* **10**: 247–267.

Darlington, C. D., 1964. *Genetics and man.* George Allen and Unwin, London.

Darwin, C., 1859. *The origin of species by means of natural selection.* John Murray, London.

Darwin, C., 1862. *The various contrivances by which orchids are fertilized by insects.* John Murray, London.

Dobzhansky, T., 1935. A critique of the species concept in biology. *Philosophy of Science* **2**: 344–355.

Dobzhansky, T., 1937. *Genetics and the origin of species.* Columbia University Press, New York.

Dobzhansky, T., 1940. Speciation as a stage in evolutionary divergence. *American Naturalist* **74**: 312–321.

Dobzhansky, T., 1950. Mendelian populations and their evolution. *American Naturalist* **84**: 401–418.

Dobzhansky, T., 1951. *Genetics and the origin of species,* 3rd edn. Columbia University Press, New York.

Dobzhansky, T., 1962. *Mankind evolving.* Yale University Press, New Haven.

Dobzhansky, T., 1970. *Genetics of the evolutionary process.* Columbia University Press, New York.

Dobzhansky, T., 1976. Organismic and molecular aspects of species formation. *In:* Ayala, F. J., ed., *Molecular evolution,* pp. 95–105. Sinauer Associates, Sunderland, Mass.

Eldredge, N. and Gould, S. J., 1972. Punctuated equilibria, an alternative to phyletic gradualism. *In:* Schopf, T. J. M., ed., *Models in paleobiology.* Freeman, Cooper and Company, San Francisco.

Ellegard, A., 1958. *Darwin and the general reader.* Gothenburg Studies in English, VIII, Goteborg.

Erickson, R., 1951. *Orchids of the west.* Paterson Brokensha, Perth, Western Australia.

Fisher, R. A., 1930. *The genetical theory of natural selection.* Oxford University Press, Oxford.

Futuyma, D. J., 1979. *Evolutionary biology.* Sinauer Associates, Sunderland, Mass.

Ghiselin, M. T., 1974. *The economy of nature and the evolution of sex.* University of California Press, Berkeley.

Greenwood, P. H., 1965. The cichlid fishes of Lake Nabugabo, Uganda. *Bulletin of the British Museum (Natural History) (Zoology)* **12**: 315–357.

Grine, F. E., 1981. Trophic differences between 'Gracile' and 'Robust' Australopithecines: A scanning electron microscope analysis of occlusal events. *South African Journal of Science* **77**: 203–320.

Gulick, J. T., 1905. *Evolution, racial and habitual.* Carnegie Institute of Washington Publication No. 25.

Hull, D., 1973. *Darwin and his critics.* Harvard University Press, Cambridge, Mass.

Irving-Bell, R. J., 1983. Cytoplasmic incompatibility within and between *Culex molestus* and *Cx. quinquifasciatus* (Diptera: Culicidae). *Journal of Medical Entomology* **20**: 44–48.

Kuhn, T., 1970. *The structure of scientific revolutions,* 2nd edn. University of Chicago Press, Chicago.

Lack, D., 1974. *Evolution illustrated by waterfowl.* Blackwell Scientific Publications, Oxford.

Lewis, K. R. and John, B., 1964. *The matter of Mendelian heredity.* J. & A. Churchill, London.

Loftus-Hills, J. J., 1975. The evidence for reproductive character displacement between the toads *Bufo americanus* and *B. woodhouseii fowleri. Evolution* **29**: 368–369.

Maslow, A., 1970. *Motivation and personality.* Harper and Row, New York.

Masters, J., Lambert, D. and Paterson, H., 1984. *Perspectives in biology and medicine.,* **28**: 107–116.

Maynard Smith, J., 1981. Macroevolution. *Nature, London* **289**: 13–14.

Mayr, E., 1942. *Systematics and the origin of species.* Columbia University Press, New York.

Mayr, E., 1949. Speciation and systematics. *In:* Jepsen, G. L., Mayr, E. and Simpson, G. G., eds, *Genetics, paleontology, and evolution,* pp. 281–298. Princeton University Press, Princeton.

Mayr, E., 1963. *Animal species and evolution.* Harvard University Press, Cambridge, Mass.

Mayr, E., 1970. *Populations, species, and evolution.* Harvard University Press, Cambridge, Mass.

Mayr, E., 1976. *Evolution and the diversity of life.* Harvard University Press, Cambridge, Mass.

Mayr, E., 1982. *The growth of biological thought.* Harvard University Press, Cambridge, Mass.

Mayr, E. and Provine, W. B., 1980. *The evolutionary synthesis.* Harvard University Press, Cambridge, Mass.

Miles, S. J., 1977. Laboratory evidence for mate recognition behaviour in a member of the *Culex pipiens* complex (Diptera: Culicidae). *Australian Journal of Zoology* **25**: 491–498.

Moore, J. A., 1957. An embryologist's view of the species concept. In: Mayr, E., ed., *The species problem,* pp. 325–338. American Association for the Advancement of Science Publication No. 50, Washington.

Morris, D., 1970. *Patterns of reproductive behaviour.* Jonathan Cape, London.

Packard, A., 1972. Cephalopods and fish: the limits of convergence. *Biological Reviews* **47**: 241–307.

Paterson, H. E., 1968. Evolutionary and population genetical studies of certain Diptera. Ph.D. thesis, University of the Witwatersrand, Johannesburg.

Paterson, H. E., 1973. Animal species studies. *Journal of the Royal Society of Western Australia* **56**: 31–36.

Paterson, H. E. H., 1978. More evidence against speciation by reinforcement. *South African Journal of Science* **74**: 369–371.

Paterson, H. E. H., 1980. A comment on 'mate recognition systems'. *Evolution* **34**: 330–331.

Paterson, H. E. H., 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. *South African Journal of Science* **77**: 113–119.

Paterson, H. E. H., 1982*a*. Perspective on speciation by reinforcement. *South African Journal of Science* **78**: 53–57.

Paterson, H. E. H., 1982*b*. Darwin and the origin of species. *South African Journal of Science* **78**: 272–275.

Paterson, H. E. H. and Macnamara, M. 1984. The recognition concept of species. *South African Journal of Science* **80**: 312–318.

Robson, G. C., 1928. *The species problem.* Oliver and Boyd, Edinburgh.

Tinbergen, L., 1939. Zur Fortpflanzungsethologie von *Sepia officinalis* L. *Archives Neerlandaises de Zoologie* **3**: 323–364.

Tinbergen, N., 1951. *The study of instinct.* Oxford University Press, Oxford.

Van Valen, L., 1973. A new evolutionary law. *Evolutionary Theory* **1**: 1–30.

Vrba, E., 1984. Evolutionary pattern and process in the sister-group Alcelaphini-Aepycerotini (Mammalia: Bovidae). *In:* Eldredge, N. and Stanley, S. M., eds, *Living fossils,* pp. 62–79. Springer-Verlag, New York.

Wallace, A. R., 1889. *Darwinism.* Macmillan, London.

Walter, G. H., Hulley, P. E. and Graig, A. J. F. K., 1984. Speciation, adaptation and interspecific competition. *Oikos* **43**: 246–248.

White, M. J. D., 1978. *Modes of speciation.* W. H. Freeman, San Francisco.

Wiens, J. A., 1977. On competition and variable environments. *American Scientist* **65**: 590–597.

Williams, G. C., 1966. *Adaptation and natural selection.* Princeton University Press, Princeton.

Wilson, L. G., 1970. *Sir Charles Lyell's scientific journals on the species question.* Yale University Press, New Haven.

Young, J. Z., 1975. *The life of mammals.* Oxford University Press, Oxford.